HERMAPHRODITISM IN ECHINOIDS[1]

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In his chapter on "Hermaphroditism" Goldschmidt (1923, p. 165) speaks of this as "the most unsatisfactory chapter in the whole sex problem, and up to date our material is insufficient to permit of a correct genetic or physiological understanding." The problem is still further rendered difficult by the fact that it cannot be dealt with experimentally. In the echinoids hermaphroditism, as a rule, is shown by entire gonads of an individual being of one sex or the other, *i.e.*, testes and ovaries in the same animal. More rarely ovarian and testicular tissues develop side by side in the same gonad—an ovotestis. In the five gonads radially symmetrically disposed, all possible combinations have been found, the rarest being the ovotestis.

Such a condition is of sufficiently infrequent occurrence to be noted in the literature in a number of cases in which it has been observed. The paucity of known cases is well expressed by E. B. Harvey (1939, p. 74): "Among the many thousands of *Arbacia punctulata* opened in the course of ten summers at Woods Hole, and many hundreds of *Arbacia pustulosa, Sphaerechinus granularis, Paracentrotus lividus,* and *Parechinus microtuberculatus* opened during several springs at Naples, and many hundreds of *Strongylocentrotus drobachiensis* from Maine, I observed last summer for the first time an hermaphroditic sea urchin, an *Arbacia punctulata* opened on July 4, 1938."

This situation renders an analysis of the phenomenon difficult, and the impossibility of attacking the problem experimentally prevents a precise causative analysis. Nevertheless, an examination of the cases described, the frequency of their incidence geographically and in the classification may give some clue to the phenomenon of what may be called "accidental hermaphroditism." It is hoped that this collection of records may serve to stimulate an interest in the problem and result in further information being published.

At the present time very few statistical records of bisexual echinoids are available. H. B. Moore (1932) reported one hermaphrodite in 3000 *Echinus esculentus* opened during the season 1931–32 at Port Erin. Shapiro (1935) kept an exact account of the *Arbacia punctulata* which he opened during the summer of 1935. He found one hermaphrodite in 2350 animals opened. Albert Tyler (personal communication) at Corona del Mar has kept the most extensive records and reports that 10,000 *Strongylocentrotus purpuratus* opened over a period of several years yielded approximately 20 hermaphrodites, or 1 in 500. This is the highest incidence so far reported. Tyler found that, in addition to normal development as the result of selfing, agglutination of the sperm by autologous sea water was positive. Edward Chambers, working at Berkeley with *S. purpuratus,* in the course of two seasons observed three hermaphrodites.

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At Pacific Grove, although the use of sea urchins has gone on for many years, only one bisexual individual each of *S. purpuratus* and *S. franciscanus* has been detected. In all these cases the selfed eggs gave normal plutei.

In the specimen of *S. purpuratus* opened at Pacific Grove in December, 1950 (A.R.M.), the gonads were swollen with ripe products and easily broken. There were three ovaries, one testis and one ovotestis. None of the eggs could have been fertilized *in corpore*, since no fertilized or segmenting eggs or embryos were seen at the time the animal was opened. However, as soon as the eggs and sperm were free in the sea water, fertilization took place. Development of the selfed eggs was entirely normal, the plutei differing in no way from normals.

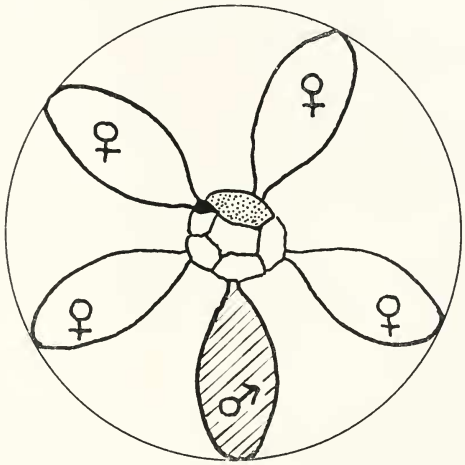

FIGURE 1. Topographical scheme showing details of female and male gonad elements of *S. franciscanus*, viewed from the aboral surface.

In March, 1955, a bisexual individual *S. franciscanus* was found (R. A. B.) at Pacific Grove. This was the first such individual of this species to be discovered. The gonads were separate as to sex, four ovaries, one testis, and no ovotestis. The distribution of the gonads is shown in Figure 1. The selfed eggs produced normal plutei as did the outcrossing of both eggs and sperm. It is to be noted that this is the first case of bisexuality found in this species. The very short breeding season may be a factor.

In addition to these examples of sea urchins, several hermaphroditic individuals of *Dendraster* have been found at Pacific Grove. The first was in 1929 (Needham and Moore, 1929), when hundreds of the animals were being used to obtain material for chemical work. In every case the entire gonadal disk was removed and any disk containing white sperm and red eggs would have been detected at once. Since only one was found, it may be assumed that the incidence was of the order of one in 1000. In this one case the eggs and sperm were not fertile *inter se*. The

second specimen of *Dendraster* was taken in 1943, and contained both ripe sperm and eggs. The spermaries occupied a little more than half the gonadal disk and yielded abundant sperm. The ovarian half contained a few ripe eggs. Less than half of these were fertilizable with the sperm of the same individual. Such eggs segmented at the normal cleavage rate and gave rise to swimming blastulae in normal time, but the plutei were not vigorous, some larvae remaining blastulae. At 55 hours and 20° C. these selfed larvae were in all stages of juvenility. It is evident that the eggs were defective in their potential, but the sperm was normal since it brought about normal development in normal eggs.

The Ovotestis

The occurrence of eggs and sperm in the same gonad has been observed in several widely different groups of animals and is a type of accidental hermaphroditism according to Goldschmidt. Ishikawa (1891) described a case in *Gebia major* in which the anterior part of the gonad was testis, the posterior part ovary. The latter was not functional since the eggs were unable to pass out through the vas deferens and consequently atrophied *in situ*. Paul Buchner (1911) described in careful detail the gonads of a bisexual starfish. He observed eggs about the sperm in the testicular vesicles, and ripe sperm infiltrated into the ovary. Harvey (1939) has shown similar conditions in a hermaphrodite *Arbacia*. All of the gonads contained both types of cells, four being mainly female, one predominantly male. Therefore all five gonads were ovotestes. Normal fertilization took place *inter se* and development proceeded to normal plutei. Similar instances have been described by Neefs (1953) and by Reverberi (1947). An account of a hermaphroditic sea urchin *S. pulcherrimus* has been published by Okada and Shimoizumi (1952), in which they give a very complete analysis. One gonad was an ovary, the others were ovotestes. The eggs and sperm did not yield normal larvae when used *inter se*, but gave normal larvae on out-crossing.

As stated above, the hermaphroditic *S. purpuratus* found at Pacific Grove contained one ovotestis. This gonad was preserved and imbedded by Dr. D. P. Abbott at this station. The specimen remained in block until the present season when it was sectioned and mounted by Mr. W. K. Bowen of the Biology Department of Stanford University. The gonad appeared to be divided into an upper and lower half which were, respectively, ovary and testis. Sections were made of parts that were clearly unisexual and of the mixed median zone. Sections of the ovarian half show the ovarian lobes well filled with eggs both ripe and immature (Fig. 2), while sections of the testicular half show normal testicular structure and dense collections of sperm in the vesicles and ducts (Fig. 3). In the median section ovarian and testicular tissue lie side by side, the acini intermingled in the same section (Fig. 4). Ripe ova occur among the sperm (Fig. 5), but no eggs were found fertilized, a fact which presumably was due to the immobility of the sperm. This duplicates the situation in the case described by Harvey.

Two clear exceptions to the general rule that fertilization does not occur *in corpore* before the extrusion of the sex cells from an ovotestis have been noted. H. B. Moore (1935) describes one such case in *Echinocardium cordatum*. In his sketches he figures apparently normal early segmentation stages, morulae and blastulae present in the gonadal ducts of the ovotestis. Reverberi (1947) has described

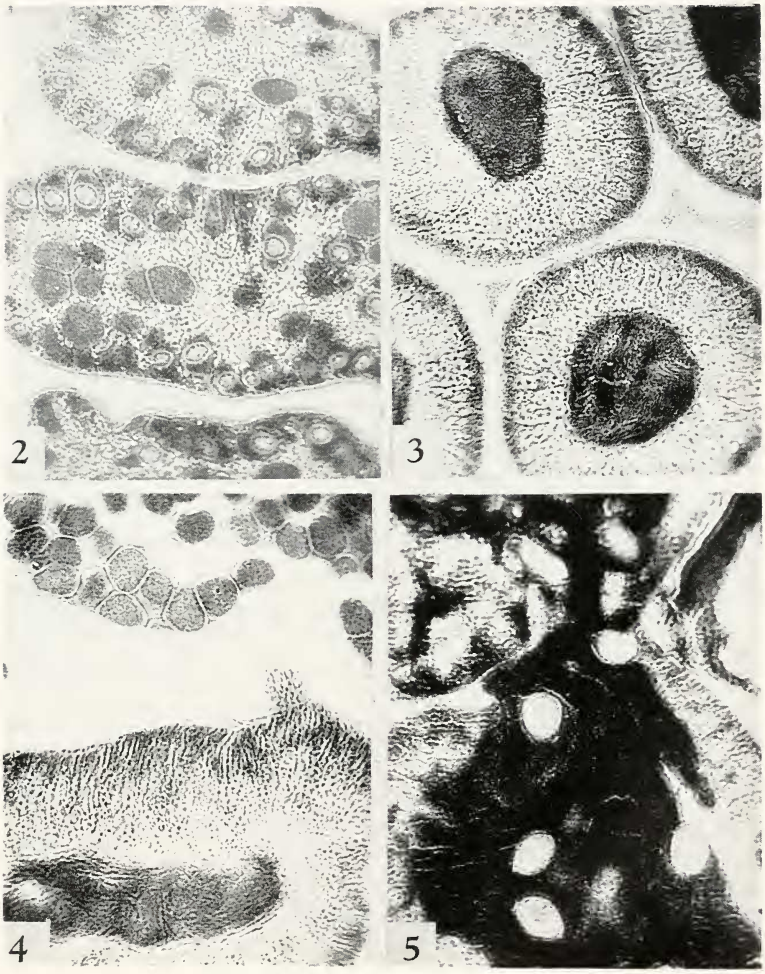

FIGURE 2. Ovarian fraction of ovotestis.
FIGURE 3. Testicular fraction of ovotestis.
FIGURE 4. Boundary zone showing ovarian tissue above, testicular below.
FIGURE 5. From boundary zone showing vesicle with eggs in mass of sperm.

a similar case in *Arbacia pustulosa* at Naples. However, Neefs' (1953) figure of a cell-mass in the lobe of an ovary of a bisexual *Arbacia lixula* is of doubtful significance, for the reason that the structure appears to be a relatively unorganized mass of cells without recognizable embryonic form, and is apparently a solitary instance in the specimen.

Discussion

Various causative factors have been proposed to account for hermaphroditism in echinoids. The oldest is the suggestion of seasonal dimorphism by Giard (1900) who, working at Wimereux, found evidence which he thought sufficient for concluding that *Echinocardium cordatum* is normally a protandrous hermaphrodite, for the reason that in July ova begin to appear in individuals which up to that time he believed had been male. However, Giard's conclusions were later emphatically denied by Caullery (1925) who states that the gonads of this form at Wimereux are entirely quiescent during autumn, the gametes developing during the winter, the phase of maturity beginning in April and ending in August, with a maximum in May. As a result of numerous observations, Caullery says (p. 29): "I have never found a single case of hermaphroditism (in this form) and I cannot explain how Giard could think that at Wimereux, *Echinocardium* shows successive sexuality with protandry, the eggs beginning to appear toward mid-July in the gonads which up to that time were apparently male and full of sperm." Since Caullery, the eminent zoologist and director of the Wimereux Station, has written from the vantage point of 25 years after Giard's paper, it must be considered established that Giard observed a rare case of hermaphroditism in *Echinocardium* (two others have been recorded at Roscoff and one at Port Erin), and that he was clearly in error in postulating seasonal sexual dimorphism for the whole population of this species. Recently Reverberi (1940, 1947) in Italy and Neefs (1937, 1938, 1952, 1953) in France have sought to revive Giard's hypothesis and give it substantial support. Reverberi considers the fact of an ovotestis in itself to be a significant indication of sexual metamorphosis. But to the unbiased worker it is not clear why the fact that normal eggs and sperm occur side by side in an ovotestis, with no evidence whatever of either type of gland degenerating, should indicate a process of sexual metamorphosis. It must be confessed that Reverberi's observations do not give convincing basis for his hypothesis. Neefs has used two lines of argument for her belief in the seasonal change of sex as the basis of bisexuality. One is the presence of degenerate gonads of two colors in an animal. Such a case was described by Gray (1921). We occasionally find them among the *S. purpuratus*. Since these pathological individuals often do not have either eggs or sperm, the more conservative view should be taken, namely, that the appearance is an indication of disease. The other attempt of Neefs to show seasonal sexual dimorphism has been made by means of statistical counts of sex. It must be said that her tables are not convincing, for the reason that at each station a relatively limited number of individuals was examined, and animals of both sexes appeared in each month of the year—a very different picture from that given by Giard. It should also be noted that no one except Giard has reported seasonal incidence of bisexuality.

Recently Egami (1955) has proposed a nutritional basis for bisexuality in fishes. He has shown that periods of starvation, succeeded by food in plentiful

TABLE I

Table of reported cases

Author	Species and cases	Locality
Normal Eggs and Sperm		
Boolootian (this paper)	*S. franciscanus*	Pacific Grove
Chambers (personal communication)	*S. purpuratus*	Berkeley
Cornman (Harvey, 1956)	*Arbacia punctulata*	Woods Hole
Fisher (Harvey, 1956)	*Arbacia punctulata*	Woods Hole
Fox (Gray, 1921)	*Paracentrotus lividus*	Naples
Giard (1900)	*Echinocardium cordatum*	Wimereux
Harvey (1939)	*Arbacia punctulata* (2)	Woods Hole
Herbst (1925)	*Psammechinus tuberculatus*	Naples
Heilbrunn (1929)	*Arbacia punctulata* (2)	Woods Hole
Herlant (1918)	*Paracentrotus lividus* (12)	Villefranche
Moore, A. R. (this paper)	*S. purpuratus*	Pacific Grove
Moore, H. B. (1932)	*Echinus esculentus*	Port Erin
Moore, H. B. (1935)	*Echinocardium cordatum*	Port Erin
Neefs (1938)	*Paracentrotus lividus* (7)	Roscoff
Neefs (1952)	*Sphaerechinus granularis*	Roscoff
Neefs (1937 and 1953)	*Arbacia lixula* (2)	Banyuls
Reverberi (1940)	*Arbacia pustulosa*	Naples
Tyler (personal communication)	*S. purpuratus* (20)	Corona del Mar
Defective Eggs—Normal Sperm		
Drzewina and Bohn (1924)	*Paracentrotus lividus*	Roscoff
	Echinocardium cordatum (2)	Roscoff
Moore, A. R. (this paper)	*Dendraster excentricus*	Pacific Grove
Normal Eggs—Defective Sperm		
Okada and Shimoizumi (1952)	*S. pulcherrimus*	Japan
Viguier (1900)	*Sphaerechinus granularis*	Algiers
Needham and Moore (1929)	*Dendraster excentricus*	Pacific Grove
Shapiro (1935)	*Arbacia punctulata*	Woods Hole
Reverberi (1947)	*Arbacia pustulosa* (5)	Naples
	Psammechinus microtuberculatus	Naples
No Test		
Chambers (personal communication)	*S. purpuratus* (2)	Berkeley
Gadd (1907)	*S. droebachiensis*	Murmansk
Rulon (personal communication)	*Dendraster excentricus*	Pacific Grove

Genus Incidence—Summary of Cases

Arbacia	15	*Dendraster*	3	*Psammechinus*	2
Paracentrotus	21	*Echinocardium*	4	*Sphaerechinus*	2
Strongylocentrotus	27	*Echinus*	1		

supply, in rare cases result in hermaphroditism. It is possible that other causative factors will have to be taken into account in any final analysis. Two of these are the incidence of hermaphroditism in the classification, and the distribution of the phenomenon geographically. On the first point, it is a striking fact that instances of hermaphroditism so far described are from relatively few genera and species, and these belong almost entirely to the order of the true sea urchins (Table I). Here we find five genera and ten species represented, while the sand dollars and

heart urchins furnish examples in one species each. One factor which may in part account for this preponderance of the true sea urchins is the accessibility and extensive use of these animals in scientific work. Most of them are littoral dwellers and are easily obtained, while members of the other two orders as a rule are dwellers of deeper waters and do not yield the quantity of eggs to be found in most of the sea urchins during the breeding season, and hence are little used. In view of the rarity of the phenomenon, the total number of individuals of a species examined is an important factor.

Despite the fact that ten or more species of sea urchins have been extensively used in experimental work, most of the cases of hermaphroditism have come from three genera, namely, *Arbacia, Paracentrotus* and *Strongylocentrotus*. It is notable that *Lytechinus*, which has been extensively used in southern stations, has not yielded a single case. Nor have examples of hermaphroditic sea urchins been reported from northern waters, except for the observation of a specimen of *S. drobachiensis* found fifty years ago at Murmansk by Gadd (1907). No cases have been reported from Scandinavia, none from Maine, none from the Oregon and Washington coasts. The distribution of hermaphroditic echinoids so far reported is in a band between N 35° and 55° in Europe, and between N 32° and 45° in North America.

More information and precise records with publication are needed to give a basis for assessing possible causative factors. It is important that those engaged in work with echinoid material examine animals opened for possible bisexuality, and where this condition is found, a sketch record be made of the positions of ovaries, testes, and ovotestes. Harvey's suggestion that cases of ovotestis may have been passed over as due to contamination when a worker has found occasional fertilized eggs among those freshly shed, is worth bearing in mind. Experiments to determine developmental potentialities both *inter se* and in outcrossing are of great interest and importance.

Summary

Two new cases of hermaphroditism in sea urchins are described. In a search for causative factors of bisexuality, a survey of incidence of the phenomenon in echinoids, both as to genera and geographical distribution, has been made. The suggestion of seasonal dimorphism is rejected.

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